SYSTEMATIC PLACEMENT OF LYCAENA COGINA SCHAUS (LEPIDOPTERA: LYCAENIDAE: POLYOMMATINAE), A BIOGEOGRAPHICALLY DISJUNCT NEW WORLD SPECIES

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Abstract.—Bálint and Johnson described genus Elkalyce in the Lycaenopsis Section of the Polyommatini for the South American butterfly Lycaena cogina Schaus and suggested that it is closely related to the tropical Asian Oreolyce Toxopeus. This systematic placement was based on four characters that are phylogenetically uninformative or incorrect. A medial uncus without lateral hairy lobes, cephalad entry of the ductus ejaculatorius into the penis, and brief anastomosis of forewing veins Sc and R₁ further falsify this systematic placement. Elkalyce cogina is transferred to the Everes Section of the Polyommatini following an unpublished hypothesis from the late John Eliot, where it is likely a close relative, perhaps a congener, of the primarily eastern Asian Tongeia Tutt. Elkalyce and Tongeia are the only genera with "false" alulae, which we characterize morphologically, on the male genitalia penis, but the position of the "false" alulae in each genus is slightly different. A lectotype is designated to preserve stability of the name Lycaena cogina Schaus, and the distribution and habitat of E. cogina are summarized. Six cases are noted in which a New World lycaenid species, or species pair, is most closely related to an Old World lineage, but E. cogina is the only endemic South American lycaenid whose closest relative is in the Old World. Whether or not Elkalyce is congeneric with Tongeia, the relict distribution of *E. cogina* suggests extinction in the intervening areas.

Key Words: Elkalyce, Everes Section, false alulae, Lycaenopsis Section, Polyommatini, Tongeia

Schaus (1902) described *Lycaena cogina* from southern Brazil (Castro, Paraná). Even though *Lycaena* Fabricius was widely used at that time for species now placed in subfamily Polyommatinae (Draudt 1919–1921, Eliot 1973), Schaus did not suggest those polyommatine species to which *L. cogina* might be most closely related. Bálint and Johnson (1996) described genus *Elkalyce* for *L. cogina* in the *Lycaenopsis* Section of the Polyommatini (Eliot 1973, Eliot and Kawazoé 1983). They noted that *Elkalyce* is not congeneric with other New World genera, but suggested that it is most closely related to *Oreolyce* Toxopeus, a genus that occurs primarily in the tropical parts of Asia. Alternatively, John N. Eliot examined a male of *Lycaena cogina*, including its genitalia, and proposed that it is related to *Tongeia* Tutt in the *Everes* Section of the Polyommatini (unpublished letters to Robbins, January 1988), a genus that occurs primarily in temperate and subtropical parts of Asia. Eliot died in 2003 without publishing this hypothesis (Eliot and Barlow 2003).

The first purpose of this paper is to publish the evidence supporting Eliot's hypothesis. Roger Vila and colleagues (Museum of Comparative Zoology, Harvard University) are sequencing parts of the DNA of Polyommatini worldwide with special emphasis on the Neotropical fauna. When the DNA of *E. cogina* is sequenced (it has not yet been sampled; Vila, personal communication), phylogenetic analysis of the sequence data can then be compared with the different morphological hypotheses of Eliot and of Bálint and Johnson.

The second purpose of this paper is to summarize and make available information about the poorly known *E. cogina*. We illustrate adults of *E. cogina* because they were not figured in the major compendia of Neotropical lycaenid butterflies (Draudt 1919–1921, D'Abrera 1995). We also designate a lectotype for *E. cogina* and summarize information on its distribution and habitat.

The third purpose of this paper is to summarize those cases in which a New World lycaenid species, or species pair, is most closely related to species in the Old World. This summary serves as background information for assessing the biogeographic significance of the distribution of *E. cogina*.

MATERIALS AND METHODS

The results in this paper are based primarily upon an examination of 23 specimens of *E. cogina* in the National Museum of Natural History (USNM), Smithsonian Institution, Washington, DC, USA, and in the Museu de Zoologia (MZSP), Universidade de São Paulo, SP, Brazil (Appendix). The genitalia of two males of *E. cogina*, one male of *Tongeia fischeri* (Eversmann), and one male of *Oreolyce quadriplaga* (Snellen) were dissected using standard entomological techniques (Robbins 1991). Genitalic terminology follows Klots (1970) except for the terms uncus and uncus lobes, which follows Eliot (1973) and Eliot and Kawazoé (1983). Venation was studied using standard techniques (Robbins 1991) and illustrated using digital scanning. Vein terminology follows Eliot and Kawazoé (1983). The distribution of *E. cogina* was determined from 86 specimens in MZSP, USNM, and DZUP (Universidade Federal do Paraná, Curitiba, Brazil) plus literature citations, as noted in the Appendix. Notes on the habitat of *E. cogina* are based on the literature and on fieldwork by the authors in the states of São Paulo, Minas Gerais, and Rio de Janeiro.

RESULTS AND DISCUSSION

Does *Elkalyce cogina* belong to the *Lycaenopsis* Section of the Polyommatini?

Bálint and Johnson (1996: 345) based their hypothesis that E. cogina belongs to the Lycaenopsis Section on four characters: (1) hindwing tailless, (2) male genitalia with uncus lobes produced, (3) vinculum with a pronounced subtriangular extension directed cephalad, and (4) caecum more or less developed, suprazonal portion short. The Lycaenopsis Section has been revised worldwide, including figures of adults and genitalia (Eliot and Kawazoé 1983), and we illustrate the male genitalia of E. cogina (Fig. 1) and Oreolyce quadriplaga (Fig. 2). Oreolyce is the genus suggested by Bálint and Johnson (1996) to be a close relative of E. cogina in the Lycaenopsis Section.

More than 20 of the 30 sections of the Polyommatini include tailless species (Eliot 1973), so the first character listed by Bálint and Johnson (1996) provides little phylogenetic information. The second character does not distinguish the *Lycaenopsis* Section from other sections (Eliot and Kawazoé 1983). Further, the full character description is "male genitalia with uncus lobes usually produced, sometimes to a stout spike, and turned inwards and downwards" (Eliot 1973: 449). *Oreolyce quadriplaga* (Fig. 2) has uncus lobes that fit this description. Although the medial uncus of

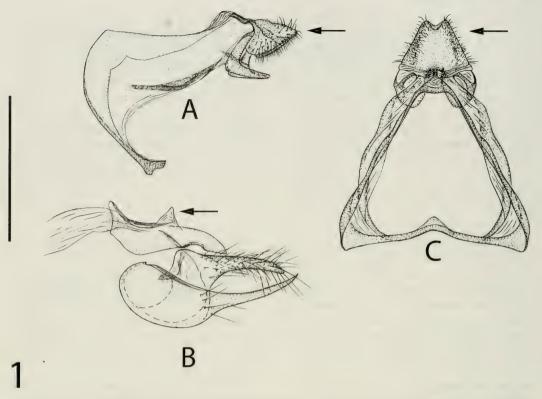


Fig. 1. Male genitalia of *Elkalyce cogina*. A, lateral aspect of genital capsule, arrow points to the uncus. B, lateral aspect of penis and valva, arrow points to false alula. C, dorsal aspect of genital capsule, arrow points to the uncus. Scale 0.5 mm.

E. cogina is posteriorly produced (Fig. 1), there are no lobes that are produced inwards and downwards. The "vinculum hump" character was defined as "a triangular or semicircular projection on the proximal side of the vinculum" (Eliot and Kawazoé 1983: 16). This structure is conspicuous in O. quadriplaga (Fig. 2, additional figures in Eliot and Kawazoé 1983). It is questionable whether the curved vinculum of E. cogina (Fig. 1) fits this definition, but if so, it is significantly less pronounced than the Lycaenopsis Section. The caecum of the Lycaenopsis Section (Fig 2, additional. figures in Eliot and Kawazoé 1983) is lacking in E. cogina (Fig. 1). In support of these results, the illustrations of the male genitalia of E. cogina in Bálint and Johnson (1996) (their figs. 3-5) do not show (1) uncus lobes turned inwards and downwards as

they are in the *Lycaenopsis* Section, (2) a vinculum hump equivalent to that in the *Lycaenopsis* Section, or (3) a caecum.

Other character information from the male genitalia and wing venation also falsify the hypothesis of Bálint and Johnson (1996). A comparison of the male genitalia uncus of Elkalyce and Oreolyce in dorsal aspect (Figs. 1C, 2C) shows little morphological similarity. The uncus of E. cogina is a medial, posteriorly produced process (Fig. 1), but the uncus in the Lycaenopsis Section is a transverse band that is laterally extended into paired hairy lobes (Fig. 2, ~100 genitalic illustrations in Eliot and Kawazoé 1983). The ductus ejaculatorius enters the cephalad side of the penis in E. cogina (Fig. 1), but enters the dorsal side of the penis in the Lycaenopsis Section (Fig. 2, Eliot 1973). Forewing veins Sc and R_1

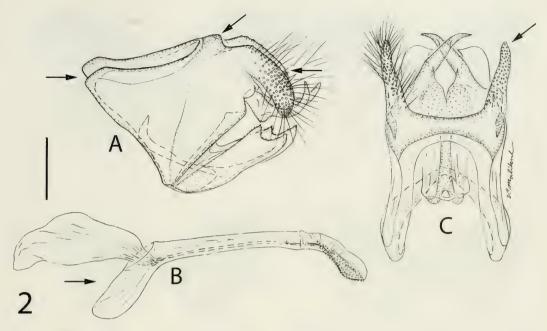


Fig. 2. Male genitalia of *Oreolyce quadriplaga*. A, lateral aspect of genital capsule, arrow at left points to the "vinculum hump," arrow on top points to the uncus, arrow at right points to the lobes of the uncus. B, lateral aspect of penis, arrow points to the caecum. C, dorsal aspect of genital capsule, arrow points to the lobes of the uncus. Scale 0.5 mm.

anastomose and separate in *E. cogina* (Fig. 4), but do not anastomose in the *Lycaenopsis* Section (Eliot 1973, Eliot and Kawazoé 1983).

In summary, there is no substantive morphological evidence to support the placement of *Elkalyce cogina* in the *Lycaenopsis* Section.

Does *Elkalyce cogina* belong to the *Everes* Section of the Polyommatini?

In contrast to the *Lycaenopsis* Section, taxonomy within the *Everes* Section of the Polyommatini has not been revised on a worldwide basis and is somewhat chaotic. For example, although Tutt (1908) differentiated *Everes* Hübner and *Cupido* Schrank, these names have recently been treated as subgenera without phylogenetic argument falsifying Tutt's classification (Hesselbarth et al. 1995, De Prins and Iversen 1996). We quote from John Eliot's letter to Robbins (14 January 1988) and present the supporting evidence for his hypothesis that *E. cogina* is closely related to *Tongeia* in the *Everes* Section.

"The possession of a distinct uncus, narrowly bifid at the apex, must put it [E. cogina] into ... the Everes Section ..., with which its other characters of venation, eyes, palpi, etc. are consistent. The genitalia are ... remarkably similar to those of Tongeia Tutt, 1908, a primarily eastern Palaearctic Everid genus, even down to the false "alulae" on the penis, of which Tutt (1908: 43) says: "the aedoeagus itself ... has a marked raised zone ... where supported." This feature cannot be seen in his Plate II, fig. 3, wherein the photographed genitalia are very distorted. However, excellent figures of Tongeia genitalia can be found in Shirozu (1960) and Kawazoe & Wakabayshi (1976)."

The male genitalia of *E. cogina* (Fig. 1) and *Tongeia fischeri* (the type species of *Tongeia*) (Fig. 3) are phenetically similar (also illustrated on page 170 in Kawazoé and Wakabayshi 1976), as noted by Eliot, and have "false" alulae. Nabokov (1945:

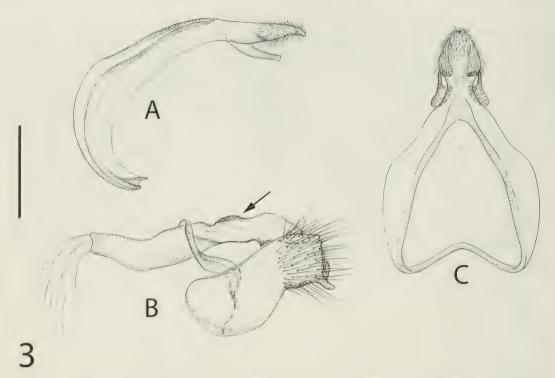


Fig. 3. Male genitalia of *Tongeia fischeri*. A, lateral aspect of genital capsule. B, lateral aspect of penis and valva, arrow points to false alula. C, dorsal aspect of genital capsule. Scale 0.5 mm.

48) introduced the term alulae to describe "out-turned flaps of subzonal sheath," and it was later defined in the glossary to Klots (1970: 221) as "paired flaps of manica, lat-

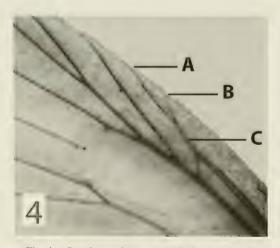


Fig. 4. Basal, anterior part of *Elkalyce cogina* forewing (digitally scanned). A, terminus of vein R_1 . B, terminus of vein Sc. C, anastomosis of veins Sc and R_1 .

erad of its attachment to the aedoeagus" (figs. 119, 121 in Eliot 1973). Alulae are sclerites of the manica and occur in the *Euchrysops* and *Polyommatus* Sections of the Polyommatini (Eliot 1973). The "false" alulae of *Tongeia* and *Elkalyce* are outgrowths of the outer wall of the phallus, perhaps the same structure that Snodgrass (1935) termed the lepidopteran theca. Whatever the homology, they are not sclerites of the manica, which is presumably why Eliot referred to them as "false" alulae.

"False" alulae are known only in *Tongeia* and *Elkalyce*. They are unrecorded in other genera of the *Everes* Section, specifically in *Everes, Cupido, Bothrinia* Chapman (= *Bothria* Chapman), *Shijimia* Matsumura, *Talicada* Moore, and *Binghamia* Tutt (Chapman 1908, Tutt 1908, Shirôzu 1960, Eliot 1973, Kawazoé and Wakabayshi 1976). The male genitalia of *Tiora* Evans do not seem to have been illustrated,

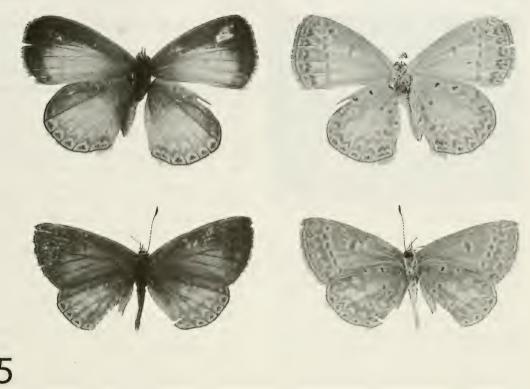


Fig. 5. Male and female *Elkalyce cogina*. Female on top. Dorsal surface on left. Female is the lectotype. Female forewing length 10.5 mm.

but *Tiora* has been considered a junior subjective synonym of *Everes* (Hesselbarth et al. 1995).

As noted by Eliot, the morphology of *E.* cogina is consistent with the characterization of the *Everes* Section as outlined in Eliot (1973). Forewing veins Sc and R_1 anastomose briefly (Fig. 4), the hindwing is tailless (Fig. 5), battledore scales are absent (*E. cogina* and *Tongeia* males lack both androconia and blue scales dorsally), the eyes are smooth, the palpi are hairy, and the male genitalia are typical of the *Everes* Section (cf. fig. 116 in Eliot 1973).

Although the evidence presented in the preceding paragraphs supports a close relationship between *Tongeia* and *Elkalyce*, we do not synonymize them. The "false alulae" of *Tongeia* (Fig. 3, male genitalic illustrations of other *Tongeia* species in Shirôzu 1960) are more posterior than those of *E. cogina* (Fig. 1), casting some doubt on their homology. Characters of the female genitalia are likely to be an important line of evidence in the placement of *Elkalyce*, but documenting female genitalic structures in the *Everes* Section is beyond the scope of this small project. However, if new evidence supports the monophyly of *Tongeia* + *Elkalyce*, *Elkalyce* should be synonymized because monotypic genera are of dubious classificatory value (Farris 1976).

Nomenclature.—To preserve stability of the name *Lycaena cogina* Schaus, we designate as **lectotype** a female with a red type label corresponding with the original description (Type No. 5920) and a handwritten label (*Lycaena cogina* Schs type) from Castro, Paraná (Figs. 5–6). A male and a female with the same red type label are from São Paulo and Rio de Janeiro states, respectively (Appendix), and lack the word "type" on the handwritten label. Since the original description noted only Castro, Pa-

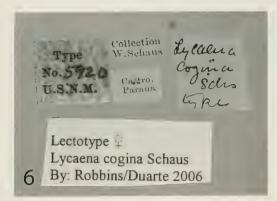


Fig. 6. Labels on the lectotype.

raná, Brazil, these two are not types. A fourth specimen has a "Castro, Paraná" locality label of the same kind as the lectotype. Although it lacks a red type label, it could be a type (Appendix). Since the original description did not mention the number of specimens, our lectotype designation makes the name bearing type of this name clear.

Habitat and distribution.—Brown and Mielke (1967: 151) noted that *E. cogina* is "partial to marshy areas" in the central plateau of Brazil. In our limited experience with this species, it occurs not uncommonly in open areas, whether disturbed roadsides, cerrado vegetation, or grasslands, albeit, always in the vicinity of wetlands. It is recorded from 500 to 1,700 m elevation. Dates of capture include most months of the year, but no captures have been recorded in October and November.

Elkalyce cogina occurs widely in the central plateau of Brazil (south of 10°S latitude), southern Brazil, and northeastern Argentina (Fig. 7, Appendix). Bálint and Johnson (1996: 344) gave the distribution of *E. cogina* as "known only from Paraná, Brazil at present." Anomalously, they ex-



Fig. 7. Distribution of Elkalyce cogina based on specimens and literature citations in the Appendix.

amined specimens from Campos de [sic] Jordão, São Paulo, Brazil, and cite Hayward (1973) and Ebert (1969), who recorded *E. cogina* from Misiones, Argentina and Poços de Caldas, Minas Gerais, Brazil, respectively. Further, Brown and Mielke (1967) had recorded it from many other Brazilian localities. Other than *Elkalyce*, the only New World genus in the *Everes* Section is *Everes*, which occurs from Canada to the lowlands of Costa Rica and Panama (Godman and Salvin 1889, Robbins unpublished) and is more than 4,000 km distant from the known range of *E. cogina*.

Disjunct New World Lycaenidae.-Although some lycaenid genera are Holotropical (e.g., Leptotes Scudder, Zizula Chapman) (Clench 1964, Eliot 1973) or Holarctic (e.g., Satyrium Scudder, Callophrys Billberg) (Clench 1961), there are six cases in which a New World lycaenid species (or non-sympatric species pair) is most closely related to an Old World lineage. Using the classification of Eliot (1973) and the recent overview of the Neotropical Lycaenidae (Lamas 2004a, b, c; Robbins 2004), these cases are (1) the North American Miletinae, Feniseca targunius (Fabricius), whose wing pattern, male genitalia, and pupal shape closely resemble Spalgis Moore in the African and Oriental Regions (Eliot 1973), (2) the North American Theclinae. Habrodais grunus (Boisduval) (including H. poodiae Brown & Faulkner in Baja California), which is probably most closely related to the Iratsume Sibatani & Ito in temperate Asia (Shirôzu and Yamamoto 1956), (3) the North American Theclinae, Hypaurotis crysalus (Edwards), which is probably most closely related to the Palearctic Favonius Sibatani & Ito and Quercusia Verity (Shirôzu and Yamamoto 1956), (4) the montane Guatemalan and Mexican Lycaeninae, Iophanus pyrrhias (Godman and Salvin), whose wing pattern, male foreleg, and genitalia resemble those of Melanolycaena Sibatani from montane New Guinea (Sibatani 1974), (5) the Polyommatinae genus Brephidium Scudder, which occurs in the Antillean Basin (*Brephidium pseudofea* [Morrison]), the Nearctic (*B. exilis* [Boisduval]), and South Africa (Eliot 1973), and (6) the South American Polyommatinae, *Elkalyce cogina*, which belongs to the primarily Palearctic *Everes* Section and may be congeneric with the primarily temperate Asian *Tongeia*.

There is currently a healthy controversy concerning disjunct butterfly taxa and whether current distributions are due to vicariance or dispersal (e.g., de Jong 2003, Hall et al. 2004, Braby et al. 2005). Elkalyce cogina is the only endemic South American lycaenid whose closest relatives are in the Old World. It is the only case in the butterflies, of which we are aware, in which a species restricted to eastern South America is most closely related to lineages in temperate Asia. Whether or not E. cogina belongs to Tongeia, its relict distribution suggests extinction in the intervening areas, as was recently shown with an amber fossil and its extant relatives in the Riodinidae (Hall et al. 2004).

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APPENDIX

Specimens examined and literature citations for *Elkalyce cogina* (museum acronyms in Materials and Methods). If elevation was not recorded on a specimen's data label, we parenthetically note the elevation for that locality as it is listed in gazetteers.

BRAZIL (north to south): DISTRITO FED-ERAL. 1 ♂ Southwest of Sobradinho (Sobradinho River), 1,025 m, 12 August 1965 (Brown and Mielke 1967: 151); 1 9 Brasília, Fazenda Água Limpa [an ecological station of the University of Brasília] (1,000-1,200 m), 22 May 1976 (USNM); 1 ♂ Brasília, Ribeirão da Contagem (1,100 m), 23 February 1966 (DZUP); 1 & same locality, 25 February 1966 (DZUP); 1 ♂ Brasília, no specific locality, 23 February 1968 (DZUP); A number of δ and \Im , Brasília, Jardim Zoológico de Brasília, 1,020 m, 8 June 1966 (Brown and Mielke 1967: 151); 3 ♂ and 4 ♀ Brasília, Reserva Ecológica do IBGE (1,000-1,200 m), 23 March 1987 (DZUP).

Gotás. 1 $\stackrel{\circ}{\circ}$ Campinas [suburb of presentday Goiânia] (800 m), March 1930 (MZSP); A number of $\stackrel{\circ}{\circ}$ and $\stackrel{\circ}{\circ}$, 30 km north of Brasília (Maranhão River), 700 m, 12 June 1966 (Brown and Mielke 1967: 151); 1 $\stackrel{\circ}{\circ}$ 30 km north of Brasília (Maranhão River), 700 m, 17 August 1965 (Brown and Mielke 1967: 151); 1 \checkmark Goiás Velho [also known as "Goiás," city of the state of Goiás, 144 km north of Goiânia. 15°57'S, 50°07'W] (500 m), 30 May 1976 [genitalia dissection by J. N. Eliot] (USNM); 1 \checkmark same locality, 20 June 1976 [genitalia dissection by R. K. Robbins] (USNM); 1 \updownarrow Vianópolis (1,000 m), March 1930 (MZSP).

MINAS GERAIS. 1 9 Paraopeba, 3 km east of BR-040 (Paraopeba Woods), 750 m, 7 June 1966 (Brown and Mielke 1967: 151); 5 ♂ Catas Altas, Caraca, 1,300–1,500 m. 1-5 February 1985 (DZUP); 1 ♂ same locality, 1,300 m, 4-6 February 2003 (DZUP); 1 ♂ Carmo do Rio Claro (859 m), 20 February 1959 (DZUP); 1 ♂ Barbacena, 1,100 m, 20 July 1951 (DZUP); 1 ♂ same locality, 9 August 1951 (DZUP); 1 9 Varginha (600-1,000 m), February 1972 (DZUP); Several specimens, Pocos de Caldas, 1,000-1,500 m, February, April and May (Ebert 1969: 41); 1 9 15 km southeast of Itamonte, 22°21.8'S, 44°47.5'W, 1,450 m, 25 April 1994 (USNM).

RIO DE JANEIRO: 1 \bigcirc Teresópolis, Parque Nacional Serra dos Órgãos, 22°27'S, 43°00'W, 1,100 m, 16 February 1995 (USNM); 1 \bigcirc Itatiaia, Parque Nacional do Itatiaia, 22°27'S, 43°37'W, 1,100 m, 5 May 1995 (USNM); 2 \heartsuit Petrópolis, São José (800–900 m), 30 February 1954 (DZUP); 1 \heartsuit Petrópolis (800 m), no date (USNM, from Schaus Collection, with a red label "Type No. 5920 U.S.N.M.," but is not a type—see text).

SÃO PAULO: 1 δ Rio Claro, 600 m, 23 June 1963 (USNM); 1 δ Serra Negra (1,000 m), 24 September 1957 (DZUP); 1 \Im same locality, 12 September 1957 (DZUP); 2 δ Campos do Jordão, 1,600 m, 26 January 1966. Cited in Bálint and Johnson (1996: 344); 6 δ and 1 \Im same locality, Parque Estadual de Campos do Jordão, 1,600–1,700 m, 22–25 January 1992 (DZUP); 1 \Im Itatiba (760–785 m), December 1935 (MZSP): 1 \Im Serra do Japi, 23°15'S, 46°54'W, 1,100 m, 12 April 1991 (USNM); 1 \Im São Paulo, "Matto do Governo" [presently known as "Parque do Estado" including both the Zoological and Botanical Parks] (760 m), February 1914 (MZSP); 1 & same locality, May 1919 (MZSP); 1 & São Paulo, Santo Amaro [a neighborhood of the city of São Paulo] (760 m), 1 ° April 1945 (MZSP); 1 ° same locality, 24 December 1958 (MZSP); 1 ♂ same locality, 26 December 1958 (MZSP); 1 & São Bernardo do Campo (762 m), 29 April 1927 (MZSP); 1 ♂ Batatais (733 m), 25 December 1968 (DZUP); 1 ♀ São Paulo, no specific locality, no date (MZSP); 1 8 São Paulo, no specific locality, no date (USNM, from Schaus Collection, with a red label "Type No. 5920 U.S.N.M.," but is not a type-see text).

PARANÁ. 1 $\[mathcal{P}\]$ Castro (999 m), no date (USNM, from Schaus Collection, with a red label "Type No. 5920 U.S.N.M.," designated **lectotype**); Sex undetermined (no abdomen or forelegs), same locality, no date (USNM); 2 $\[mathcal{d}\]$ same locality, Ribeira, 530

m, 20 December 2002 (DZUP); 2 & Ponta Grossa, no specific locality, May 1947 (DZUP); 1 9 same locality, Olaria (700 m), no date (DZUP); 2 δ and 1 \Im same locality, Piriquitos (900 m), 3 April 1971 (DZUP); 1 ♂ same locality, Rio Bonito (900 m), March 1947 (DZUP); 1 9 Campina Grande do Sul, Jaguatirica, 1,000 m, 27 February 2003 (DZUP); 1 ♂ Jaguariaíva (850 m), April 1951 (DZUP); 8 ♂ and 4 ♀ Campo Largo, Três Córregos, 700 m, 7 March 1998 (DZUP); 1 ♂ same locality, 30 km north of Bateias (880 m), 4 March 2000 (DZUP); 1 9 Balsa Nova, São Luiz do Purunã, 900-1,000 m, 8 March 1980 (DZUP); 1 ^Q same locality, 25 February 1984 (DZUP); 2 9 same locality, 12 April 1986 (DZUP).

RIO GRANDE DO SUL. 1 $\stackrel{\circ}{_{\sim}}$ no specific locality, no date (MZSP).

ARGENTINA: Misiones, no specific locality (Hayward 1951: 142). Canals (2003) added no new information on *E. cogina* in Misiones.